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Do Transmission Isolating Mechanisms (TRIMS) influence cultural evolution? Evidence from patterns of textile diversity within and between Iranian tribal groups

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Introduction

There are important differences in the ways that genes and cultural traits can be transmitted among human individuals. Whereas genes can only be transmitted “vertically” from parents to children, cultural practices and ideas can be acquired from a variety of sources (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985). While the ethnographic record demonstrates that many craft skills, subsistence techniques and other important cultural behaviours are vertically transmitted (e.g. Hewlett and Cavalli-Sforza 1986; Shennan and Steele 1999; Greenfield et al. 2000; Ohmagari and Berkes 1997; Lozada et al. 2006), it also shows that learners often acquire specialised knowledge from unrelated members of the older generation such as teachers, master craftsmen, etc. (“oblique transmission”) (e.g. Aunger 2000; Hewlett and Cavalli-Sforza 1986; Henrich and Gil-White 2001, Ohmagari and Berkes 1997, Reyes-Garcia et al. 2009; Tehrani and Collard 2009a). In addition, individuals can copy traits from unrelated members of their own generation (“horizontal transmission”).

In view of these differences, many anthropologists have assumed that patterns of cultural evolution are bound to be far more complex and intertwined than patterns of genetic evolution (Boas 1940, Kroeber 1948, Terrell 1988, Moore 1994). Recently, however, this assumption has been challenged by a number of researchers (e.g. Durham 1990, 1992; Mace and Holden 2005; Collard et al. 2006; Tehrani and Collard 2009a). One of the most influential of these critiques was developed by William Durham (1990, 1992). Durham argued that whereas cultural transmission within groups is facilitated by common language, intermarriage and shared social norms, transmission between groups is often constrained by ecological boundaries, language barriers, endogamy, rivalry/warfare, in-group conformity and xenophobic attitudes. He termed these factors “Transmission Isolating Mechanisms” (TRIMS), analogous to the reproductive isolating mechanisms that prevent gene flow between species. Contrary to the classical view in anthropology, Durham proposed that the prevalence of TRIMS in the ethnographic record indicates that societies usually inherit the bulk of their cultural traits from their ancestors through branching processes of descent with modification (“phylogenesis”). Thus, despite the differences in genetic and cultural transmission between individuals, the processes involved in generating between-group cultural similarities and differences are, according to this view, fundamentally similar to the processes that give rise to biodiversity.

Durham’s hypothesis is consistent with a number of recent empirical studies suggesting that phylogenesis has played an important role in generating cultural and linguistic

diversity among populations (e.g. Collard et al. 2006, Mace et al. 2005, Lipo et al. 2006). However, only one of these studies directly examined the role played by TRIMS in generating these patterns. The study in question was one we carried out some years ago on the evolution of textile designs among a group of Turkmen tribes in of north-eastern Iran, Turkmenistan and Afghanistan (Tehrani and Collard 2002). We examined weavings produced during two periods of Turkmen history. The first period was prior to the military conquest of the Turkmen by Imperial Russian forces in the 1880s, during which time the Turkmen practiced a nomadic-pastoralist lifestyle. The second period was after the Russian colonisation, which led to the forced settlement of the Turkmen and the increasing commercialisation of craft production. Cladistic analyses of rug designs suggested that phylogenesis dominated the evolution of Turkmen rug traditions in both periods. These results were consistent with ethnohistorical data, which indicated that cultural transmission among the tribes is likely to have been inhibited by two important TRIMS, namely endogamy and endemic warfare. At the same time, we found evidence that the rate of borrowing increased when these constraints were weakened following the Russian conquest (after which the tribes were forcibly pacified and gradually became politically and economically integrated into the new regime).

While the results of our Turkmen study supported the proposal that TRIMS play a major role in cultural phylogenesis, the hypothesis makes other important predictions that have yet to be studied empirically. One of these is that patterns of cultural diversity between groups should exhibit greater phylogenetic structure than patterns within groups. Here, we present a study that was specifically designed to test this prediction.

The study focused on woven textiles produced by tribal populations in western Iran. Textile weaving is the dominant craft activity in these communities and is carried out exclusively by females. Ethnographic evidence suggests that there are likely to be powerful TRIMS that constrain the transmission of weaving knowledge between tribes (Tehrani and Collard 2002, 2009a, 2009b). First, the tribes, or *ll*, are organized into territorially distinct political/ethnic groupings, and were until recently frequently in conflict with each other and the Iranian state (e.g. Barth 1961; Beck 1986; Garthwaite 1983). Secondly, intermarriage between the tribes was prevented by norms of tribe endogamy. This is likely to be particularly relevant to the transmission of weaving because core craft skills are transmitted vertically from mother to daughter. Given that girls are almost always born into their mothers' natal tribes, this means that new weaving techniques from other groups are rarely introduced into the tribe (Tehrani and Collard 2009a). Endogamous marriage is likely to also

influence the transmission of designs. Unlike techniques, designs are frequently learned through oblique and horizontal transmission among women in the same community (Tehrani and Collard 2009a). The main way in which weavers come into contact with women belonging to other communities is when they get married and move to their husband's village. Since they marry into villages belonging to the same tribe, this would not be expected to lead to the transmission of patterns between tribal groups.

While social organization and marriage practices are likely to have operated as TRIMS on between-group craft transmission, we hypothesize that they probably encouraged the circulation of weaving traits within tribes. Members of the same tribe (*Il*) recognised a common leader, the *il khan*, who had the power to raise taxes and recruit armies from the patrilineal clans (*tayfeh*) that constituted the tribe. Disputes between the clans over migration routes, pasture or water resources would either be resolved by the leaders of the groups involved (*kadkhodas*), who were directly responsible for these issues, or when necessary mediated by higher-level authorities (such as the *il-khan* or his deputies, the *il beg*). This quasi-legal system helped to maintain the unity of the tribe and ensure harmony among its consistent parts. Consequently, whereas we expect cultural transmission between tribes to have been inhibited by the hostile character of their relationships, the co-operative institutions that existed within tribes would have facilitated exchanges between clans. Similarly, while endogamous marriage would be expected to prevent the transfer of weaving traits between tribes, it would not inhibit the flow of traits among clans. Although individuals often express a preference for marriage between patrilineal relatives, marriages between members of different patrilines are far from uncommon. For example, Digard (2002:22) estimates that marriages between patrilineal relatives accounts for only 18 – 43% of all marriages. In the field, JJT encountered many cases where women married into another patriline.

In sum, Iranian weaving traditions provide an ideal context in which to test Durham's TRIMS hypothesis. Based on the ethnographic data outlined above, we predict that patterns of craft diversity between tribes will exhibit greater phylogenetic structure than patterns of craft diversity between clans belonging to the same tribe.

Materials and methods

Data on between-group patterns of textile diversity comprised designs associated with communities belonging to four tribes in south-western Iran: the Bakhtiari, Qashqai, Papi and Boyer Ahmad (Figure 1). The weavings of the Bakhtiari, Qashqai and Boyer Ahmad were

sampled during a survey of craft production in the Zagros Mountains conducted by JJT over the course of three visits to the area between May 2001 and June 2003. The weavings of the Papi were studied through a catalogue of the extensive collections of Papi material culture held at the Copenhagen Museum of Ethnography published by Mortensen and Nicolaisen (1993). A total of 80 designs were recorded on rugs, woven bags and blankets, and packing bands produced by these groups (Figure 2). The presence/absence of each design in each tribe was recorded in a matrix.

FIGURES 1 & 2 ABOUT HERE

Data on within-group patterns of textile diversity was drawn from rug designs associated with five communities belonging to the Bakhtiari tribe. Each community comprised between one and three villages belonging to the same patrilineal clan. The communities were situated in the districts of Chehelgerd, the Chahar Mahal valley, Bazoft, Boldaji and Aligudarz. The weavings of these communities were sampled during two field trips to the region in April-July 2002 and May 2003. A total of 50 carpet ornaments were identified and recorded for each tribe on a presence/absence basis.

Both datasets were analysed using the cladistic method of phylogenetic reconstruction. Cladistics has been widely used in biological (e.g. Kitching et al. 1998; Page & Holmes 1998; Schuh 2000), linguistic (Ben Hamed et al. 2005; Gray & Jordan 2000; Holden 2002; Rexová et al. 2003) and cultural studies (e.g. Buchanan & Collard 2007, 2008; Collard et al. 2006; Cochrane 2008; Eagleton and Spencer 2006; Jordan & Shennan 2003, 2009; Lycett 2007, 2009a, 2009b; Lycett et al. 2007; Robinson and O'Hara 1996; O'Brien et al. 2001; O'Brien & Lyman 2003; Robson-Brown 1996; Shennan & Collard 2005; Tehrani & Collard 2002, 2009a, 2009b). Based on a model of evolution in which new taxa arise from the bifurcation of existing ones and subsequently undergo modification, cladistics defines relationships among taxa in terms of relative recency of common ancestry. Two taxa are deemed to be more closely related to one another than either is to a third taxon if they share a common ancestor that is not also shared by the third taxon. Exclusive common ancestry is indicated by "synapomorphies". Synapomorphies are similarities among taxa that are both the result of shared ancestry and derived relative to the ancestral state for the taxa under study. Synapomorphies are distinguished from "symplesiomorphies", "autapomorphies," and "homoplasies". Symplesiomorphies are character states that are inherited from the last common ancestor shared by all the taxa under study and have not evolved subsequently.

Autapomorphies are character states that are derived relative to the ancestral state for the study group but only occur in a single taxon. Sympleisiomorphies and autapomorphies are not useful for phylogenetic reconstruction because they do not allow subgroups of taxa to be delineated. Homoplasies are derived character states that are shared by more than one taxon in a study group as a result of processes other than descent from a common ancestor, such as convergence, parallelism, or horizontal transmission across lineages.

In its simplest form, cladistic analysis proceeds via four steps. First, a character state data matrix is generated. This shows the states of the characters exhibited by each taxon. Next, the direction of evolutionary change among the states of each character is established. Several methods have been developed to facilitate this, the currently favoured being outgroup analysis (Arnold, 1981; Maddison et al., 1984). Outgroup analysis entails examining a close relative of the study group. When a character occurs in two states among the study group, but only one of the states is found in the outgroup, the principle of parsimony is invoked and the state found only in the study group is deemed to be evolutionarily novel with respect to the outgroup state. Having determined the probable direction of change for the character states, the next step in a cladistic analysis is to construct a branching diagram of relationships for each character. This is done by joining the two most derived taxa by two intersecting lines, and then successively connecting each of the other taxa according to how derived they are, or how many synapomorphies they contain. Each group of taxa defined by a set of intersecting lines corresponds to a clade, and the diagram is referred to as a cladogram. The final step in a cladistic analysis is to compile an ensemble cladogram from the character cladograms. Ideally, the distribution of the character states among the taxa will be such that all the character cladograms imply relationships among the taxa that are congruent with one another. Normally, however, a number of the character cladograms will suggest relationships that are incompatible. This problem is overcome by generating an ensemble cladogram that is consistent with the largest number of characters and therefore requires the smallest number of homoplasies to account for the distribution of character states among the taxa (Figure 3). This approach is based on the principle of parsimony, the methodological injunction that states that explanations should never be made more complicated than is necessary (Sober, 1988).

FIGURE 3 ABOUT HERE

To test the prediction that patterns of diversity at the tribe level should be significantly more tree-like than patterns of diversity at the clan level, we carried out two analyses. In the first we used the Permutation Tail Probability (PTP) test (Archie 1989). The PTP was originally proposed as a method of determining whether or not a given data set contains a statistically significant phylogenetic signal (Archie 1989, Faith and Cranston 1991). However, following criticism (e.g. Carpenter 1992), it is now considered to be a heuristic device rather than a statistical test (Kitching et al. 1998). In the PTP test, a taxonomic data set is randomly reshuffled multiple times without replacement and the length of the most parsimonious cladogram is computed after each permutation. Thereafter, the length of the most parsimonious cladogram obtained from the unpermuted data is compared to the distribution of lengths of the most parsimonious cladograms yielded by the permutations. If the original cladogram is shorter than 95% or more of the cladograms derived from the permutations, then the data set is considered to contain a phylogenetic signal. Before carrying out the PTP tests, we added scores for an outgroup to each dataset. The outgroup we employed were the weavings of the Shahsevan. Previous analyses suggest that the Shahsevan weavings belongs to a distinct but closely related tradition to the Qashqai, Bakhtiari, Boyer Ahmad and Papi assemblages (Tehrani and Collard 2009a, 2009b). The PTP tests were carried out in PAUP* 4.0 (Swofford 1998) with 10,000 permutations of each dataset. Our test prediction was that the between-group dataset would pass the PTP test while the within-group dataset would fail it.

In the second analysis, we identified the most parsimonious tree for each dataset and then compared the trees' Retention Indices. The Retention Index (RI) (Farris, 1989b; 1989b) is a measure of the number of homoplastic changes a cladogram requires that are independent of its length (Farris, 1989b; 1989b). The RI of a single character is calculated by subtracting the number of character state changes required by the focal cladogram (s) from the maximum possible amount of change required by a cladogram in which all the taxa are equally closely related (g). This figure is then divided by the result of subtracting the minimum amount of change required by any conceivable cladogram (m) from g . The RI of two or more characters is computed as $(G - S)/(G - M)$, where G , S , and M are the sums of the g , s and m values for the individual characters. A maximum RI of 1 indicates that the cladogram requires no homoplastic change, and the level of homoplasy increases as the index approaches 0. The RI is a particularly useful goodness-of-fit measure because, unlike some other measures (e.g. the Consistency Index), it is not affected by number of taxa or number of characters, and can

therefore be used to compare phylogenetic signals in different datasets and character sets. As in the PTP tests, the Shashevan were added to both datasets as an outgroup. This analysis was also carried out with the aid of PAUP* 4.0 (Swofford 1998). The test prediction in this analysis was that the RI of the inter-tribal cladogram would be higher than the RI of the intra-tribal cladogram due to a higher rate of borrowing in the latter dataset.

Results

As predicted, the PTP test found significant phylogenetic signal in the inter-tribal data ($p < 0.01$), but not in the inter-clan data ($p = 0.53$). Thus, the PTP test-based analysis supported the TRIMS hypothesis.

The cladistic analyses returned a single most parsimonious cladogram for each dataset (Figure 4.1 & 4.2). The inter-tribal cladogram suggests that the Papi, Boyer Ahmad and Bakhtiari share an exclusive common ancestor that is not shared with the Qashqai. This is consistent with the fact that these three tribes belong to the same ethno-linguistic group, the Lurs (e.g. Amanolahi 1988), whereas the Qashqai are Turkic (e.g. Oberling 1974). The cladogram also suggests that the Bakhtiari and Papi form a clade that excludes the Boyer Ahmad. At present there are no other lines of evidence with which to compare this finding. Similarly, there are currently no data to validate the phylogenetic relationships among different Bakhtiari clans suggested by the intra-tribal cladogram. The RI of the between-group cladogram was 0.70, which is high compared to the RIs returned by empirical and simulated datasets (Collard et al. 2006; Nunn et al. 2010). At 0.38, the RI of the within-group cladogram was much lower. Thus, like the PTP test-based analysis, the RI test supports the TRIMS hypothesis.

FIGURE 4.1 & 4.2 ABOUT HERE

Discussion

The results of the PTP and RI analyses support the TRIMS hypothesis, which predicts that patterns of cultural diversity between groups should exhibit greater phylogenetic structure than patterns within groups. There are, however, two potential criticisms that could be leveled at this interpretation of our results. First, some researchers have claimed that because cladistic

algorithms are designed to maximize the fit between a dataset and the tree model, a high RI, such as that obtained from the inter-tribal textile data, cannot be assumed to reflect phylogenesis (e.g. Borgerhoff Mulder et al. 2006, McElreath 2009). It has been suggested that it is possible to obtain high RI values from datasets that have actually been structured by horizontal processes, or even from random data (McElreath 2009). However, tests of these assertions have shown them to be invalid. For example, we have recently compared the RI value of the most parsimonious tree derived from an Iranian textile dataset to the RI values of the most parsimonious trees derived from 1,000 datasets that were generated by randomizing the character states (Tehrani and Collard 2009a). The highest RI obtained from the randomized datasets (0.35) was just over half the value of the RI returned by the original dataset (0.59). This indicates that cladistic analyses of random data are unlikely to produce trees with high RIs. Another study by Nunn et al. (2010) examined the RIs returned by cladistic analyses of datasets that were artificially generated under varying rates of vertical and horizontal transmission between groups. They concluded that phylogenesis can be reliably inferred when the RI is roughly equal to, or higher than, 0.6. Given that the RI of the inter-tribal textile tree (0.7) comfortably exceeds this value, we can confidently assume that between-group patterns evolved through branching descent with modification.

The second potential criticism of our conclusions is that differences in the phylogenetic signals recovered from different cultural datasets may reflect amounts of evolutionary change rather than rates of vertical versus horizontal transmission between taxa (e.g. Nunn et al. 2010). Thus, a dataset may have less phylogenetic structure than another because of the accumulation of convergences, reversals in character state changes, and so on, rather than because of borrowings. However, since the last common ancestor of the Bakhtiari clans is almost certainly of much more recent origin than the last common ancestor of the tribes, we would expect the characters in the inter-tribal dataset to have evolved much more than the characters in the inter-clan dataset. Therefore, the difference in the phylogenetic signal recovered from each dataset is much more likely to be due to rates of borrowing between clans being higher than rates of borrowing between tribes.

The findings of the study reported here are compatible with our interpretation of the results of previous analyses of textile evolution in this region. We found that between-group patterns of diversity among Turkmen tribes (Tehrani and Collard 2002) and Iranian tribes (Tehrani and Collard 2009a, 2009b) mainly evolved through phylogenesis, which we attributed to the operation of TRIMS like tribe endogamy, language barriers, restrictions on women travelling and hostile relations among groups. By confirming the importance of these

mechanisms, this study provides new evidence to support Durham's hypothesis that TRIMS produce cultural patterns similar to those that result from speciation. The corollary of this point is that when cultural datasets contain a strong phylogenetic signal, it is reasonable to infer that TRIMS are likely to have been present. Archaeological phylogenies of stone tools (e.g. Buchanan and Collard 2007, 2008; Lycett 2007, 2009a, 2009b; O'Brien and Lyman 2003), pottery assemblages (Cochrane 2008; Collard and Shennan 2000) and other artefacts might therefore provide important information for mapping the boundaries between populations and assessing their fluidity/robustness.

Likewise, when phylogenetic signals in cultural datasets are weak, this may indicate the relative absence of barriers to transmission among populations. This is supported by evidence from a study of cultural evolution in Californian Indians carried out by Jordan and Shennan (2003, 2009). These authors used cladistics, phylogenetic network analysis, correspondence analysis and Mantel tests to study the evolution of these groups' basketry traditions. They found that basket assemblages were more influenced by borrowing and blending among neighbouring groups than inheritance from ancestral populations. This is consistent with ethnohistorical data that suggested that members of these societies traded and intermarried with one another extensively. Hence, as far as the TRIMS hypothesis is concerned, Jordan and Shennan's case study can be seen as an exception that proves the rule.

Of course, the specific character and strength of TRIMS will vary from case to case, and it remains to be seen how important those that have been identified here – such as endogamy – are in other times and places. More importantly, even when powerful TRIMS do exist, they are never completely impermeable. For instance, although endogamy and social distinctions between the Iranian tribes have been effective in containing textile traits, they have provided little resistance to the spread of other behaviours, such as cigarette smoking, tea-drinking, and western medicine. Rather than identifying TRIMS with Reproductive Isolating Mechanisms in biological species, it may be more productive to think of them as a specific parameter in the diffusion of innovations that concerns the differential in the cost of learning a trait from a member of the same social group versus the cost of learning it from a member of a different social group. This would allow traits that are highly useful (e.g. antibiotics) or easy-to-acquire (e.g. smoking) to spread among populations more easily than traits that are arbitrary or difficult-to-learn (e.g. textile patterns). While such a model would require a reformulation of Durham's original conception of TRIMS, it is one that, in our view, would better capture the evolutionary dynamics of cultural diversification.

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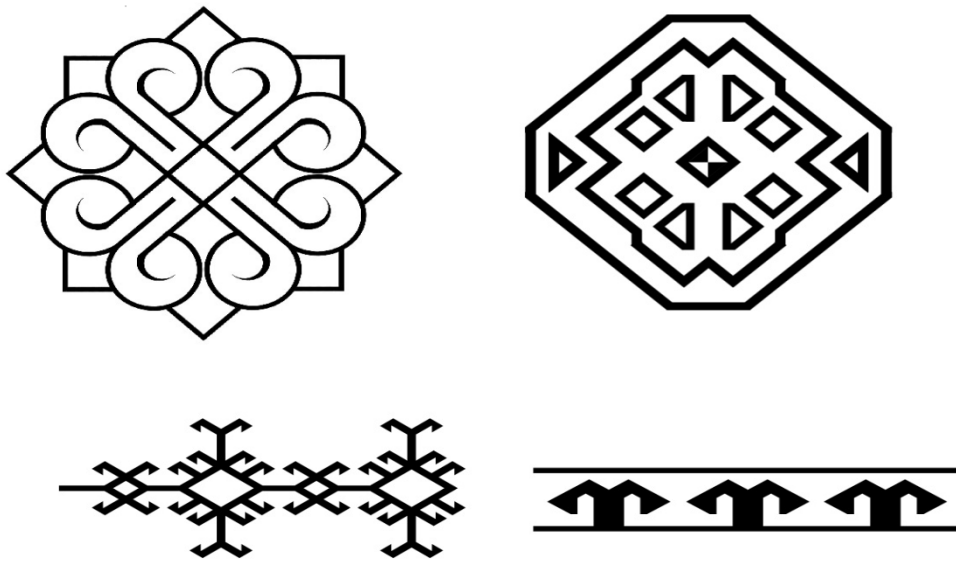


Figure 2. Examples of Iranian tribal textile ornaments (above) and border patterns (below).

	Character 1	Character 2	Character 3	Character 4	Character 5	Character 6
TAXON A	1	1	0	0	0	1
TAXON B	1	1	1	1	0	1
TAXON C	1	1	1	1	1	0
TAXON X	1	0	0	0	0	0

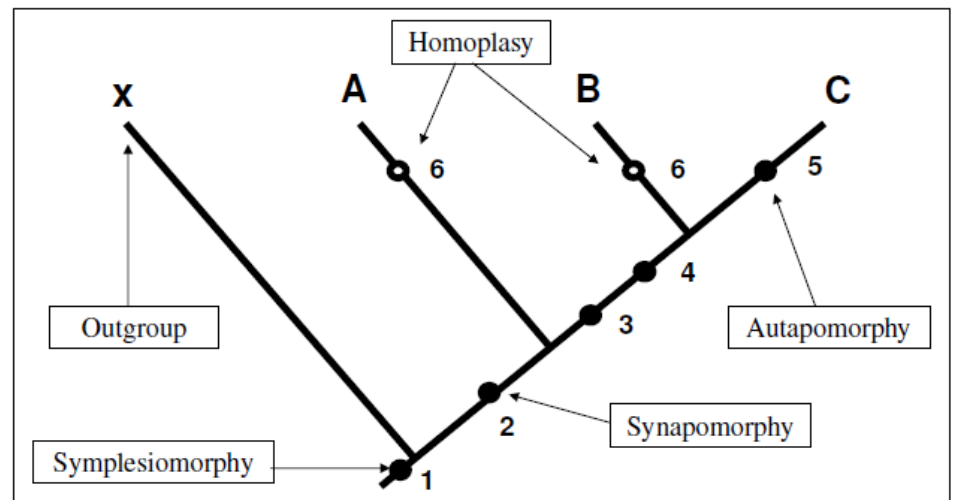


Figure 3. Ensemble cladogram derived from a hypotheticalal dataset.

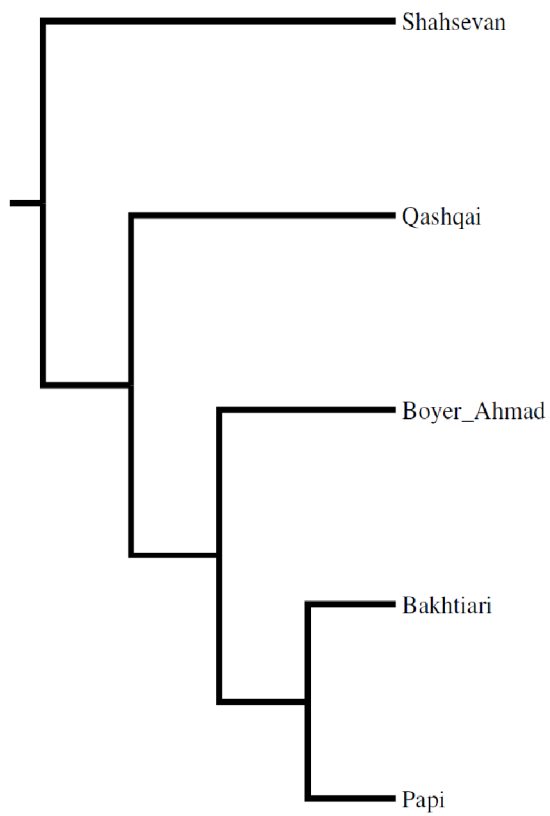


Figure 4.1. Inter-tribe textile cladogram

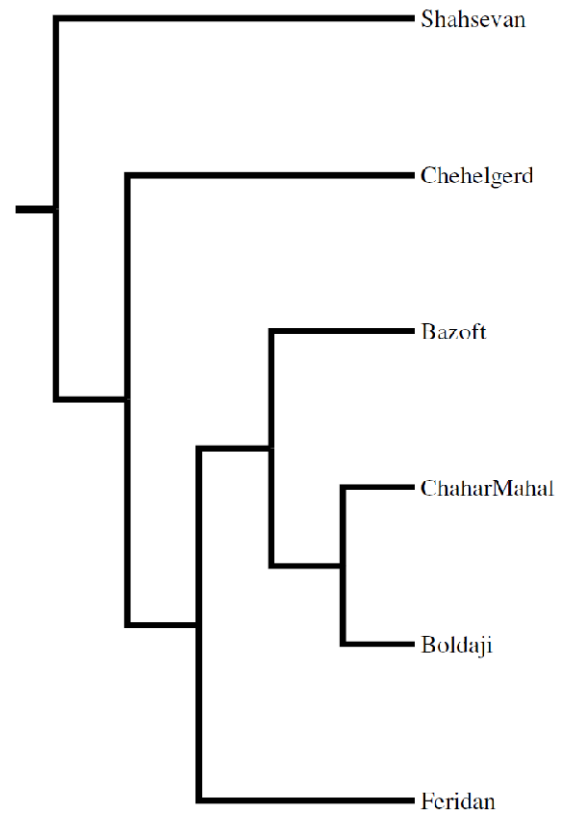


Figure 4.2 Inter-clan textile cladogram